


For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex libris
UNIVERSITATIS
ALBERTAENSIS





Digitized by the Internet Archive
in 2023 with funding from
University of Alberta Library

<https://archive.org/details/Untergasser1971>

THE UNIVERSITY OF ALBERTA

THE DEVELOPMENT OF THERMOREGULATION IN DUCKLINGS

by



GISELA UNTERGASSER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1971

ABSTRACT

The embryos of mallards and scaups show no evidence of homeothermy prior to the point of hatching. The ability to thermoregulate develops very quickly directly after hatching, so that day-old mallards remain homeothermic for at least 2.5 hrs at ambient temperatures down to $+2^{\circ}\text{C}$. The lowest ambient temperatures at which one-day old scaups and common eiders remain homeothermic for at least 2.5 hrs are -2°C and -7°C respectively. This rapid development of cold resistance is related to the peak metabolic rates and insulative capacities of which the birds are capable. In embryos of pipped eggs, metabolic rates do not exceed $1.3 \text{ ml O}_2/\text{g hr}$ for mallards and 1.6 ml/g hr for scaups, while the peak metabolic rates of the day-old young are 6.1 and 7.0 ml/g hr respectively. One-day old common eiders have a peak metabolic rate of approximately 5 ml/g hr . The mechanisms of the development of thermoregulation during the first day after hatching are not known. In all 3 species the highest peak metabolic rates are found on the third day of life. Cold resistance increases with age while peak metabolic rates decrease after an age of 3 days, indicating that reduced heat loss contributes to increased cold resistance. At an age of 10 days, mallards can maintain homeothermy for at least 2.5 hrs at -8°C , scaups at -17°C and common eiders at -19°C . Insulation indices of eider ducklings are significantly higher than those of young mallards and scaups.

The young of all 3 species survive chilling to subnormal body temperatures. In mallards, chilling to body temperatures of 20°C is tolerated to an age of at least 10 days.

The present study suggests that cold is not a critical factor for the survival of ducklings.

ACKNOWLEDGEMENTS

This study was supervised by Dr. J.S. Hayward. I want to thank him for his willingness to discuss my research, for his valuable suggestions and for the reading of the manuscript.

I am grateful to Drs. D.D. Beatty, W. Cottle, J.S. Nelson, L. Wang and A.J.F. Webster for the reading of the manuscript.

Most mallard and scaup eggs were collected by parasitology students and technicians. I wish to thank them for letting me use their specimens for my research. Special thanks are due to Mr. R. Long who spent much time to provide me with some of the latest clutches of the season. The eider eggs were obtained from Dr. C.E. Huntington, Director of the Bowdoin Scientific Station, who collected them on Kent Island, New Brunswick. I sincerely thank him for his help.

Above all, I thank my husband for his patience, encouragement and moral support during the course of this study.

Financial support for this research was obtained from a Graduate Teaching Assistantship and a Government of Alberta Graduate Scholarship.

TABLE OF CONTENTS

	Page
ABSTRACT	
ACKNOWLEDGEMENTS	
LIST OF TABLES	
LIST OF FIGURES	
INTRODUCTION	1
MATERIALS AND METHODS	4
RESULTS AND DISCUSSION	10
REFERENCES	30
APPENDIX	33

LIST OF TABLES

	Page
Table 1. Minimum body temperatures of homeothermic animals in °C	6
Table 2. Weight of ducklings 1 to 20 days old	19
Table 3. Scaup: Body composition	20

LIST OF FIGURES

	Page
Figure 1. Metabolic rates of mallard embryos 0-1 day before hatching	11
Figure 2. Metabolic rates of scaup embryos 0-1 day before hatching	11
Figure 3. Mallards: Changes in cold hardiness with age	14
Figure 4. Scaups: Changes in cold hardiness with age	15
Figure 5. Eiders: Changes in cold hardiness with age	16
Figure 6. Mallards: Changes of the peak metabolic rate with age	17
Figure 7. Scaups: Changes of the peak metabolic rate with age	18
Figure 8. Eiders: Changes of the peak metabolic rate with age	18
Figure 9. Changes in overall insulation with age	24

INTRODUCTION

Birds are homeothermic during their adult life. The temperature of their extremities may vary with the environmental temperature, but the core temperature is mostly regulated within narrow limits (Rolnik, 1948; Irving and Krog, 1955).

Precocial birds show evidence of thermoregulation shortly after hatching. The range of environmental temperatures over which homeothermy is maintained varies widely with the species. For the day-old young of galliform birds this range is quite narrow (Koskimies, 1962; Wekstein and Zolman, 1967) but increases with age until a range characteristic of the adult has been reached.

In the present study cold hardiness is defined as the ability to maintain homeothermy at low temperatures. The few papers dealing with the cold hardiness of ducklings suggest that these birds are capable of excellent thermoregulation very early in life. Koskimies and Lahti (1964) studied the young of 10 species of European ducks and found that they were all much better thermoregulators than the galliform species Koskimies had studied earlier. However, even among the anatids, there are considerable differences in cold hardiness. Generally, the young of diving ducks are more cold resistant than those of surface feeding species (Koskimies and Lahti, 1964).

Nothing is known about the onset of thermoregulation in ducks. Rolnik (1948) found that a 7 hr-old young of the common eider remained homeothermic at an ambient temperature of 8°C for at least 6 hrs, while a 2 hr-old young exposed to 5°C became hypothermic immediately and later died. This suggests that the ability to maintain homeothermy at temperatures around 8°C develops between the age of 2 and 7 hrs in the common

eider. To my knowledge nothing has been published on the thermoregulatory abilities of duck embryos, and it was unknown whether the onset of thermoregulation occurs in the embryo, or, as in altricial birds (Kendeigh, 1939) only some time after hatching. In the domestic chicken there is no sign of thermoregulation prior to hatching (Pembry, Gordon and Warren, 1895) although this species is capable of moderate thermoregulation shortly after hatching (Wekstein and Zolman, 1967). Cold hardiness can be measured directly by exposing animals to low temperatures and observing their response with respect to body temperature. These experiments indicate the lowest temperature an animal of a given age can withstand for a given period of time while maintaining homeothermy. Cold hardiness is determined by heat production and heat loss. Heat production is most easily expressed by metabolic rates, and as this study is concerned with the extent of cold hardiness, by the peak metabolic rate of which an animal is capable. These are observed at the lowest temperature at which homeothermy can be maintained. Heat loss is influenced by size and insulation (Scholander *et al.*, 1950). Size can be expressed by weight. An index of insulation can be calculated on the basis of metabolic rates and size (Scholander *et al.*, 1950). It is known from studies on the chicken (Barott and Pringle, 1946) that peak metabolic rates decrease with age. It was suspected that this decrease depends on changes in the proportion of heat producing tissues. This theory can be checked by examining animals of different ages.

The present study traces the development of thermoregulation in ducklings with respect to the extent of cold hardiness and some factors involved in the regulation of homeothermy. The species used were the mallard *Anas platyrhynchos*, the lesser scaup *Aythya affinis* and the common eider *Somateria mollissima*. The mallard was chosen because it is a common

and widely distributed species. The common eider breeds mainly in the Arctic, and I suspected that it showed an exceptionally great cold hardiness as already suggested by Rolnik's observations. The lesser scaup was chosen because it is in certain aspects intermediate between mallards and eiders. Scaups and eiders are diving ducks while mallards are surface feeders. The newly hatched scaup possesses the small size of a mallard duckling which is less than half of that of a newly hatched eider. Mallards and scaups also have a similar geographical distribution.

MATERIALS AND METHODS

Eggs of mallards and scaups were collected around various lakes and potholes within 80 miles of Edmonton, Alberta (Lat. $53^{\circ}30'N$, Long. $113^{\circ}45'W$). Eider eggs were collected on Kent Island, New Brunswick (Lat. $44^{\circ}35'N$, Long. $66^{\circ}45'W$) and shipped to Edmonton by air. All eggs were transferred to an incubator as soon as possible and incubated at $38^{\circ}C$.

Newly hatched young were transferred to a brooder when they were between 2 and 10 hrs old. All ducklings were banded and their ages were recorded to the nearest minute from the point of hatching. The time of hatching was taken as that moment when the bird freed itself completely from the egg shell. All ducklings were imprinted to the investigator to facilitate handling.

The ducklings were supplied with turkey starter¹ and water *ad libitum*. Frequently, hard-boiled, grated eggs were fed in addition. The temperature of the brooder was kept around $34^{\circ}C$ during the first day and then lowered to $30-32^{\circ}C$. When the ducklings were 3 days old, they were transferred to a cage in which one corner was supplied with a suspended heating pad, but at night they were placed for 8-10 hrs into the brooder until they were 6 days old. The ducklings were transferred to outdoor cages provided with heating pads when they were between 10 and 15 days old. The heat source was provided until the ducklings were at least 18 days old.

All ducklings were weighed daily. Their weights were plotted against their age in hours. As the ducklings were seldom weighed at exact daily intervals from the time of hatching the weights for full days were extrapolated from the graphs.

The ducklings were tested for their degree of cold resistance by

exposing them for 2.5 hrs to a given test temperature. A duckling of known age and weight was placed in a wire mesh cage which was large enough to allow some movement. The bottom of the cage was covered with some hay to absorb the droppings of the bird. The wire cage was placed in a constant temperature cabinet² where temperatures down to -22°C could be maintained. Fresh air was constantly drawn through the cold chamber, and a fan inside the chamber assured sufficient air circulation. Three birds could be studied at the same time. Thermistor probes were placed between the wire mesh cages and connected to an outside telethermometer³. All experiments were conducted with the birds in the dark. No care was taken that the ducklings were postabsorptive. Their body temperatures were measured at the beginning of an experiment with a fine thermistor probe which was pushed down the throat into the stomach. The ducklings were observed at 20 min intervals through a small window that could be opened in the door of the cold chamber. If they showed no sign of succumbing to the cold they were taken out after 2.5 hrs and their body temperatures were measured again. The minimum body temperatures at which they were defined as having withstood the test temperature are listed in Table 1. These levels were selected after a fair number of experiments had been conducted and represent those temperatures which can be maintained for a certain time without the gradual decrease which characterizes animals with insufficient cold resistance.

Ducklings with insufficient cold resistance often appeared lethargic early in the experiment. Such animals were immediately removed from the cold and checked for their body temperature. If it was below the level shown in Table 1 they were recorded as having failed the test and removed from the experiment. If their body temperature was below 37° they were

TABLE 1

Minimum body temperature of homeothermic animals in °C

Species	0-1 days	1-2 days	over 2 days
mallard	38	39	39.5
scaup	38.5	39	39.5
eider	39	39	39.5

placed in an incubator until they had recovered.

Metabolic rates were determined in an open flow respirometer. The animal was placed in an airtight container with openings for a thermistor probe and air exchange. The size of the animal chamber was selected so that the animal could only stand up and turn around. Dessicators of varying sizes and a specially designed plexiglass chamber were used to house the animal. The animal chamber was placed inside the darkened temperature cabinet. The air outlet was connected by plastic tubing to the outside of the cold chamber. Air was drawn through the animal chamber at a constant rate. For air flowrates below 300 ml/min a small pump⁴ was used while another pump was employed for higher flowrates. At flowrates up to 200 ml/min, all air drawn from the animal chamber was passed through a drying tube filled with anhydrous CaSO_4 ("Drierite") and led through a paramagnetic oxygen analyzer⁵. At higher flowrates the portion exceeding 200 ml/min was led into a bypass to the oxygen analyzer. The flowrate of the air entering the oxygen analyzer was checked by a predictability flowmeter⁶. The combined air leaving the oxygen analyzer and the bypass then passed through a second predictability flowmeter and a wet-test gas flowmeter⁷ before entering the air pump. The flowrates could be adjusted to any desired value so that the air leaving the animal chamber contained between 18 and 20% oxygen. The analysis of the air was constantly recorded⁸. Metabolic rates were expressed as oxygen consumption and calculated according to the formula

$$\text{MR} = \frac{f \cdot 60 \cdot d \cdot p \cdot 273}{t \cdot 760 \cdot w \cdot 100}$$

or

$$\text{MR} = \frac{0.2155 \cdot f \cdot d \cdot p}{t \cdot w}$$

where MR = metabolic rate in $\text{ml g}^{-1} \text{ hr}^{-1}$

f = flowrate in ml min^{-1}

d = % oxygen content of ingoing minus

% oxygen content of outgoing air

p = atmospheric pressure in mm Hg

t = room temperature in ° Kelvin

w = body weight in g

The experiments to determine peak metabolic rates were conducted for 2.5 hours as were the tests for cold resistance. The results of both series of experiments were pooled. Metabolic rates were recorded for only those birds which remained homeothermic. Failure to withstand the test temperature was mostly detected on the recording by an abnormal decline of the oxygen consumption. Ducklings showing this decline were at once checked for their body temperature and removed from the experiment if they were hypothermic.

No duckling was used on consecutive days, and in most cases 3 or 4 days elapsed before an animal was tested again. Ducklings which had become hypothermic in an experiment were not used again until at least one week had passed. A total of 19 eider ducklings, 40 mallards and 57 scaups was used.

The oxygen consumption of duck embryos was measured by the same system. An egg of a given clutch was placed in the respirometer and its O_2 consumption was measured in approximately 2° C intervals at ambient temperatures between 30 and 42° C. At least 30 minutes were allowed for the embryo to react to a new ambient temperature before the O_2 consumption was measured. The recorded metabolic rate was the average of the following 30-60 minutes. If the egg showed no sign of hatching at the end of

the experiment it was opened, the embryo was taken out and the yolk sac removed. The embryo was blotted dry on filter paper and weighed. Eggs which were pipped were allowed to hatch. The weight of the embryo was assumed to be equal to that of the 1 hr-old duckling. The age of younger embryos was estimated by letting at least 2 eggs of a clutch hatch and counting back from the average time of hatching.

Six scaups were killed with ether. From each animal the downy skin, liver with gallbladder, heart, lungs with trachea, digestive tract and spleen, fat deposits, yolk sac, kidneys and the carcass were dissected, their weights determined and recorded as % of the total body weight.

Statistical calculations are based on the equations given in Sokal and Rohlf (1969).

¹Federated Co-operatives Ltd., Calgary, Edmonton, Saskatoon, Winnipeg, Brandon.

(26.0% protein min., 3.0% fat min., 6.0% fibre max.)

²Yukon Refrigeration Service, Vancouver, B.C.

³Yellow Springs Instrument Co., Ltd., Yellow Springs, Ohio, U.S.A.

⁴German model, no trade name on instrument.

⁵Beckman Instruments, Inc., Fullerton, California, U.S.A. (Model F3M3-1AA)

⁶Monostat Corporation, New York, New York, U.S.A.

⁷Labline Instruments, Inc., Melrose Park, Illinois, U.S.A.

⁸E.H. Sargent and Co., Chicago, Illinois, U.S.A. Recorder Model MR.

RESULTS AND DISCUSSION

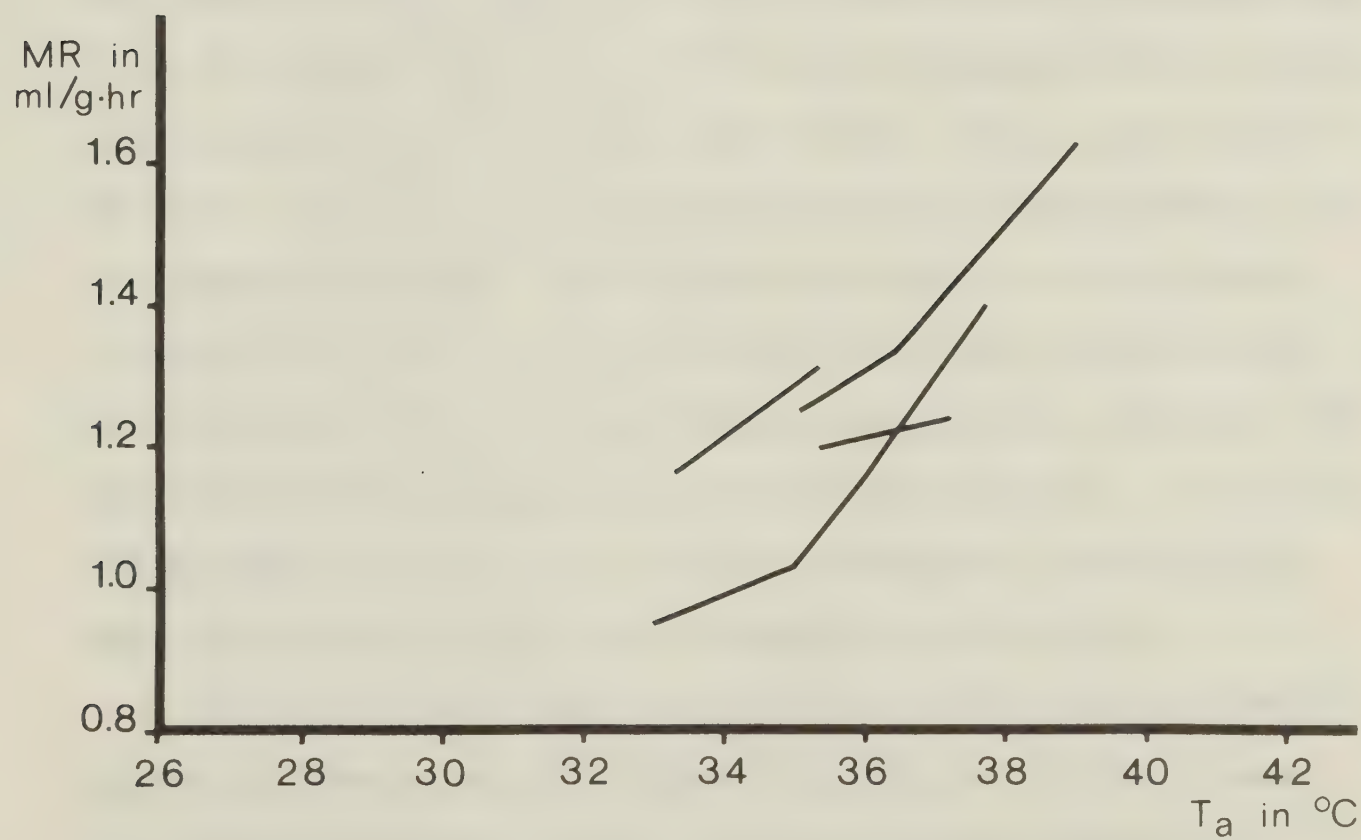
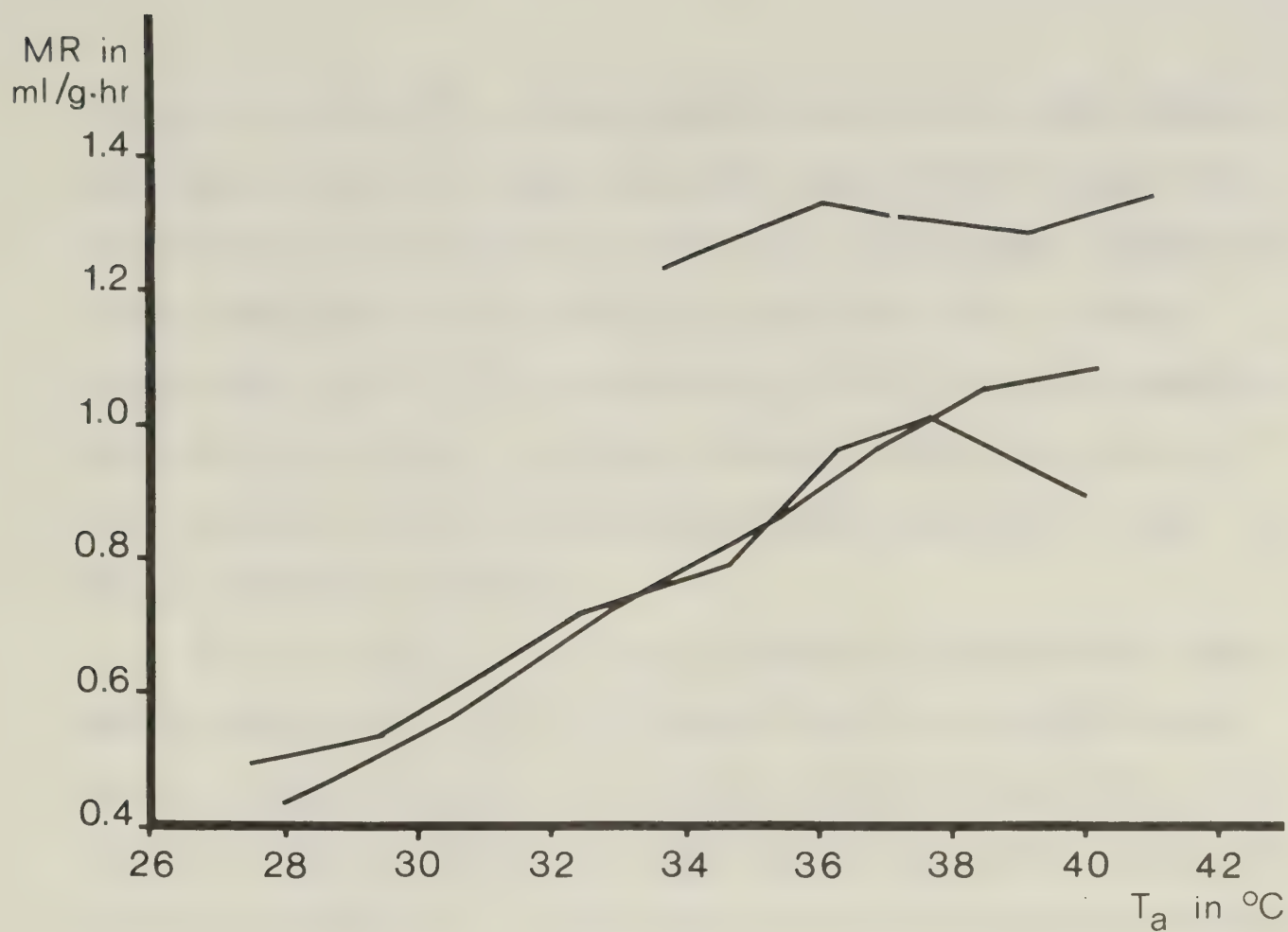
A study on thermoregulation and hypothermia of duck embryos requires a knowledge of their normal body temperatures. Unfortunately, information on this subject is scarce. Huggins (1941) implanted thermocouples into mallard eggs and found an average temperature of 34.5°C during periods of attentiveness. Barry (1967) found an average temperature of 34°C on the outside of the egg of a Pacific brant (*Branta bernicla*), and Koch and Steinke (1944) found an average temperature of 33.4°C in the nest of domestic geese. Experience with artificial incubation of chicken and duck eggs (J.K. Lauber, personal communication) suggests that 34°C may be below the normal body temperature of the embryo because best hatching results are obtained at incubation temperatures around 38°C . The body temperatures of ducklings on their first day after hatching (Table 1) also suggest that 38°C is close to the normal body temperature of duck embryos. In mallard embryos, oxygen consumption decreases if the ambient temperature is below 38°C (Fig. 1). This is true for both hatching ducklings and embryos. Thus the embryo does not respond as a homeotherm to temperatures below 38°C . The graphs for the oxygen consumption of scaup embryos are rather incomplete because all eggs hatched before the tests could be extended over a wider temperature range. The response to decreasing temperatures corresponds to that of mallards. The graphs for both mallard and scaup embryos are not as smooth as one might expect because the hatching activity of the embryo results in irregular bursts of high oxygen consumption which make it difficult to estimate the resting level of metabolism. No results are presented for eider embryos because very few eggs were available and only 2 of them were checked for signs of thermoregulation (unfortunately

Fig. 1. Metabolic rates of mallard embryos 0-1 day before hatching. Each line represents one animal.

MR = metabolic rate, T_a = ambient temperature.

Fig. 2. Metabolic rates of scaup embryos 0-1 day before hatching. Each line represents one animal.

MR = metabolic rate, T_a = ambient temperature.



only at 29.4 and 36.4°C). A more complete study of late eider embryos seems highly desirable. Some of the eider eggs which had arrived from Kent Island by air were quite warm when they were unpacked, although the ambient temperature at that time was at least below 28°C. A newly hatched eider duckling became hypothermic at 24.5°C, but it is possible that late eider embryos, in contrast to mallards and scaups, show at least a moderate degree of homeothermy at temperatures not too far removed from that of incubation.

It is not known why the oxygen consumption of mallard and scaup embryos decreases even upon such moderate chilling as provided by an ambient temperature of 35°C. Gas exchange through the egg shell may be a limiting factor. Although the oxygen consumption at 39°C exceeds that at 35°C it is probably not high enough to produce the extra heat necessary to prevent chilling upon exposure to a low ambient temperature. The chilling of the embryo then decreases its tissue metabolism which in turn allows for further chilling. Metabolic rates during periods of hatching activity often exceed the resting levels shown in Figs. 1 and 2 by 15% and more. The duckling in a pipped egg breathes at least partially with its lungs and has access to air without the barrier of the egg shell. At least in late embryos, the availability of oxygen is such that one should expect at least a moderate degree of temperature regulation. The lack of homeothermy may have survival value for the embryo. It uses its limited energy source only for growth and development and does not exhaust it by meeting the high cost of maintaining homeothermy.

The newly-hatched young of all species quickly develop an ability to maintain homeothermy at low ambient temperatures. Within 24 hours, the ambient temperature at which a constant body temperature can be

maintained for 2.5 hrs decreases by more than 30°C. The day-old mallard can withstand +2°C, the scaup -2°C and eider ducklings -7°C (Figs. 3-5).

Cold tolerance depends on the balance of heat production and heat loss. Heat production is most easily expressed by metabolic rate. Heat loss is influenced by size and surface insulation. During the first day after hatching the weight remains essentially constant so that the rapid increase in cold resistance must be explained by metabolic changes and/or changes in insulation.

The capacity for heat production exhibits a large increase during the first day after hatching (Figs. 6-8). The peak resting metabolic rates of embryos do not exceed 1.3 ml O₂/g hr for mallards (Fig. 6) and 1.6 ml/g hr for scaups (Fig. 7). The rates calculated for embryos younger than 1 day before hatching appear higher than they actually are if compared to those of older embryos and newly hatched young because the yolk sac was removed from early embryos while it constitutes a considerable portion of the body weight of a newly hatched duckling. Table 3 indicates that the day-old scaup still possesses a yolk sac of approximately 10% of its body weight. At the age of 1 day, the average peak metabolic rates are 6.1 ml/g hr for mallards, 7.0 ml/g hr for scaups and approximately 5 ml/g hr for eiders (Figs. 6-8 respectively). Mallard and scaup ducklings are similar in size at the age of 1 day (Table 2), and the better cold resistance of the scaups is at least partly explained by their higher peak metabolic rates.

The metabolic rates determined in this study are based on the weight at the beginning of the experiment. Most animals settled down quietly in the animal chamber within a few minutes, but their oxygen consumption which rose to a peak almost immediately levelled off only slowly.

Fig. 3. Mallards: Changes in cold hardiness with age. T_a = ambient temperature, dot = homeothermy maintained during 2.5 hours exposure to T_a , triangle = homeothermy not maintained. Age 0 days = time of hatching, -2 days = 2 days before hatching.

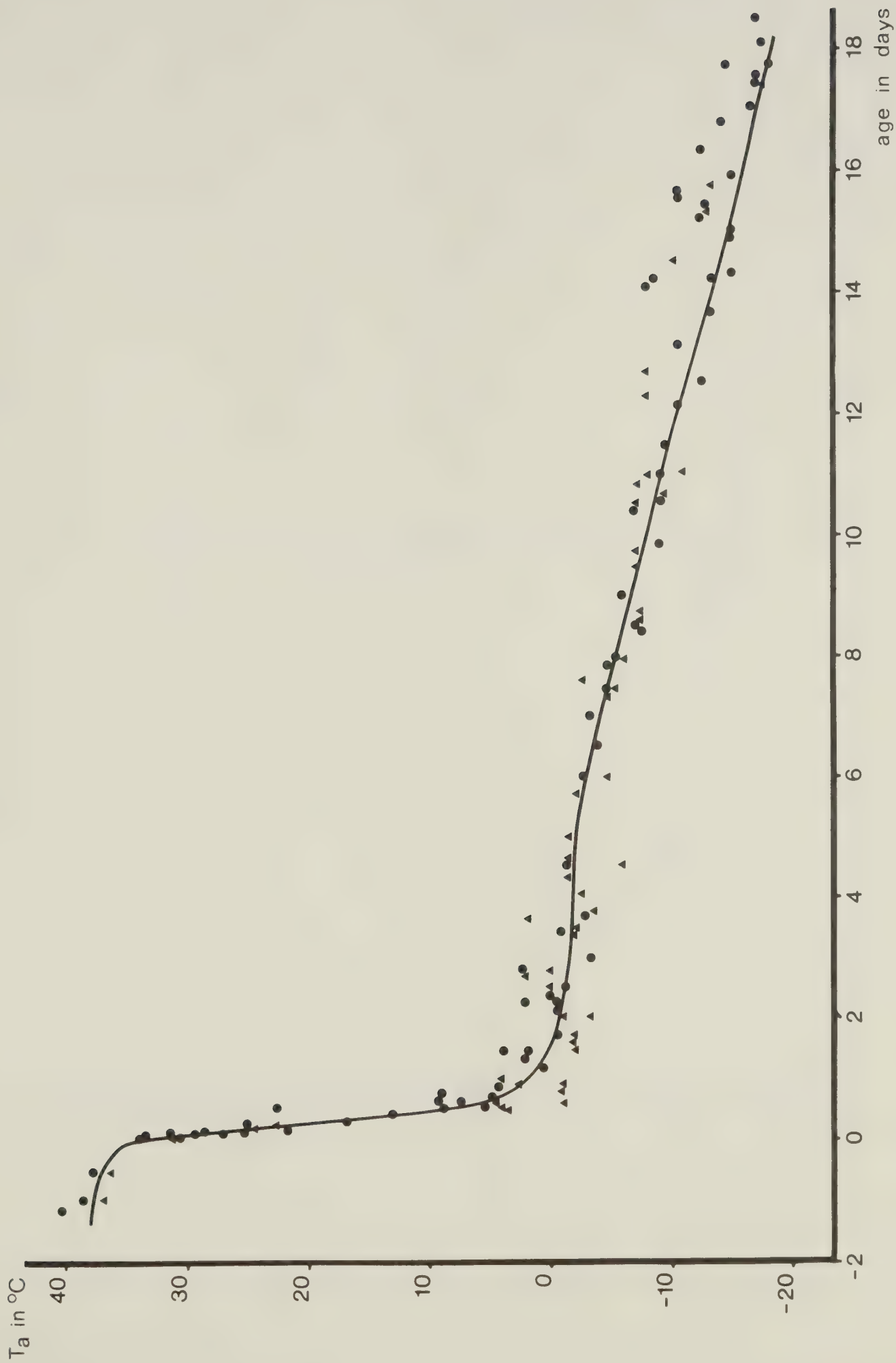


Fig. 4. Scaups: Changes in cold hardness with age. Legend as in Fig. 3.

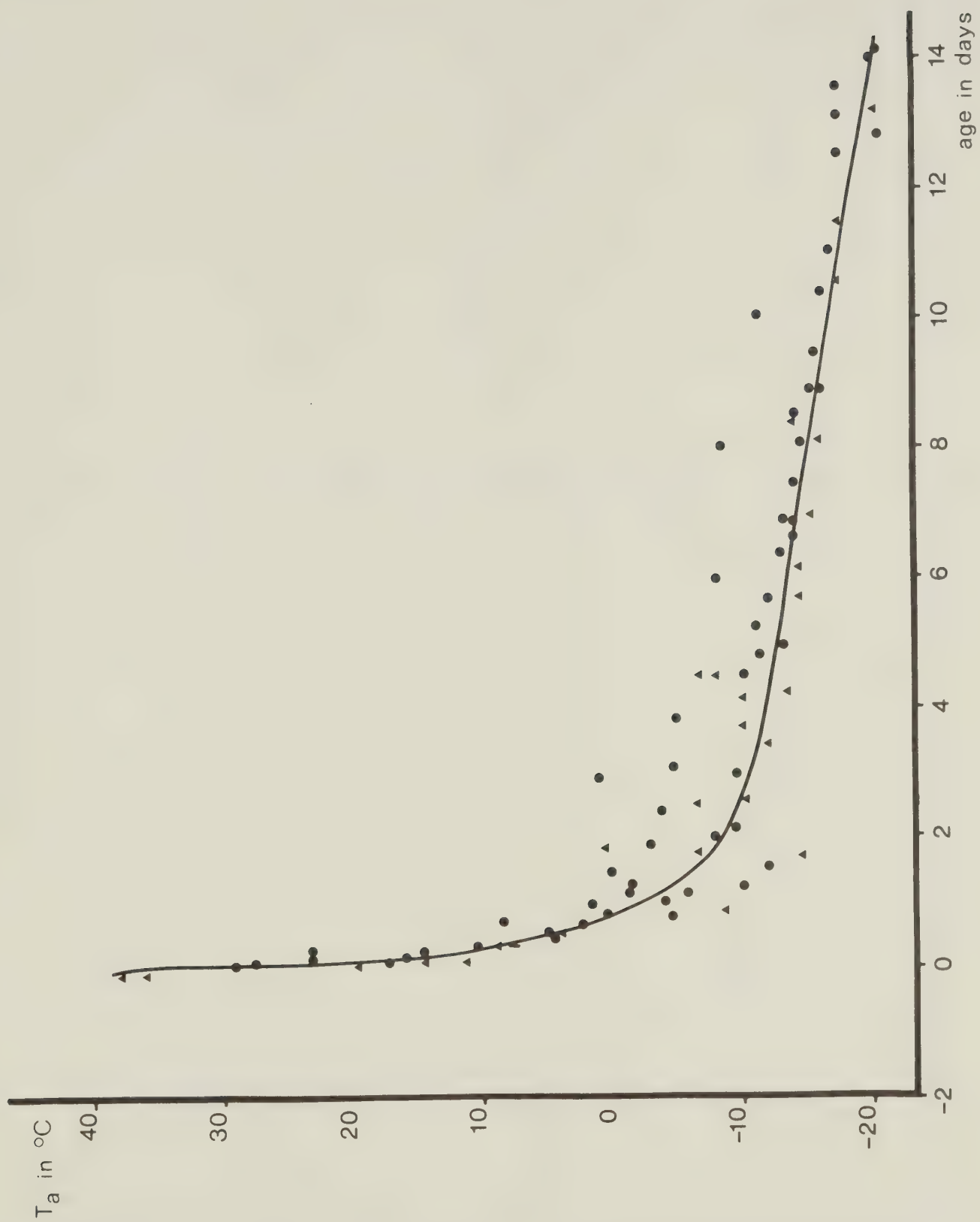


Fig. 5. Eiders: Changes in cold hardness with age. Legend as in Fig. 3.

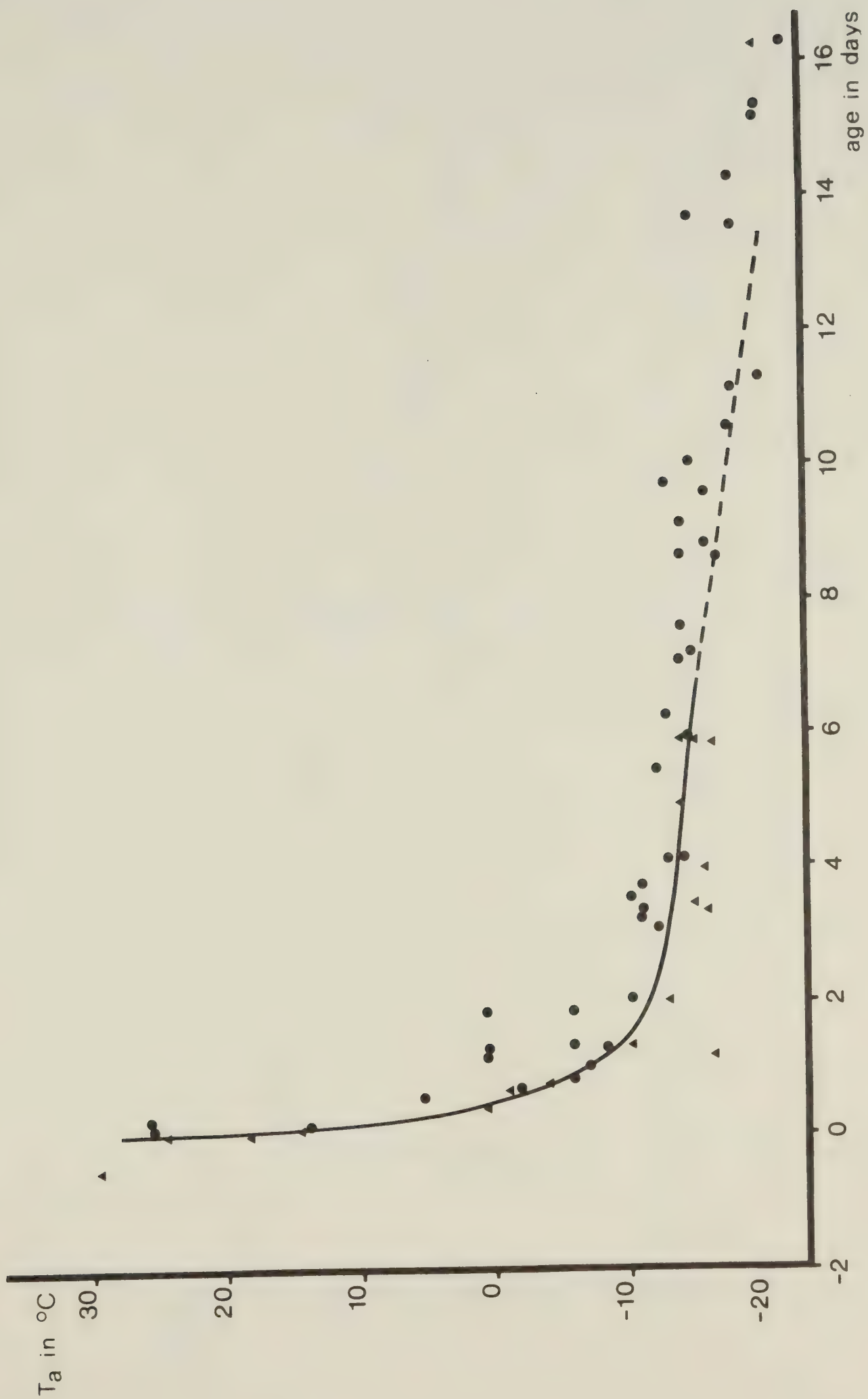


Fig. 6. Mallards: Changes of the peak metabolic rate with age.

MR = metabolic rate. The values plotted were obtained at temperatures not more than 3°C above those indicated by the line in Fig. 3.

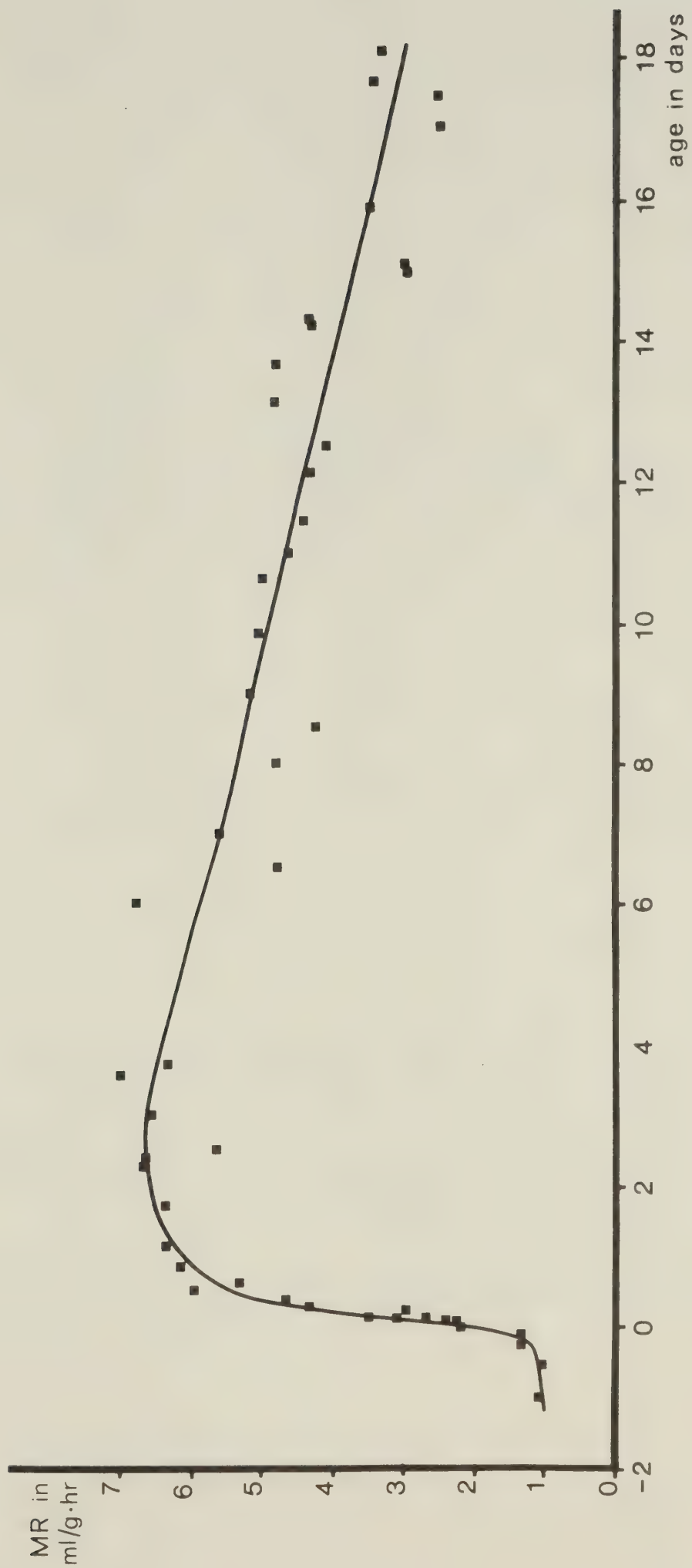


Fig. 7. Scaups: Changes of the peak metabolic rate with age.

MR = metabolic rate. The values plotted were obtained at temperatures not more than 3°C above those indicated by the line in Fig. 4.

Fig. 8. Eiders: Changes of the peak metabolic rate with age.

MR = metabolic rate. The values plotted were obtained at temperatures not more than 3°C above those indicated by the line in Fig. 5.

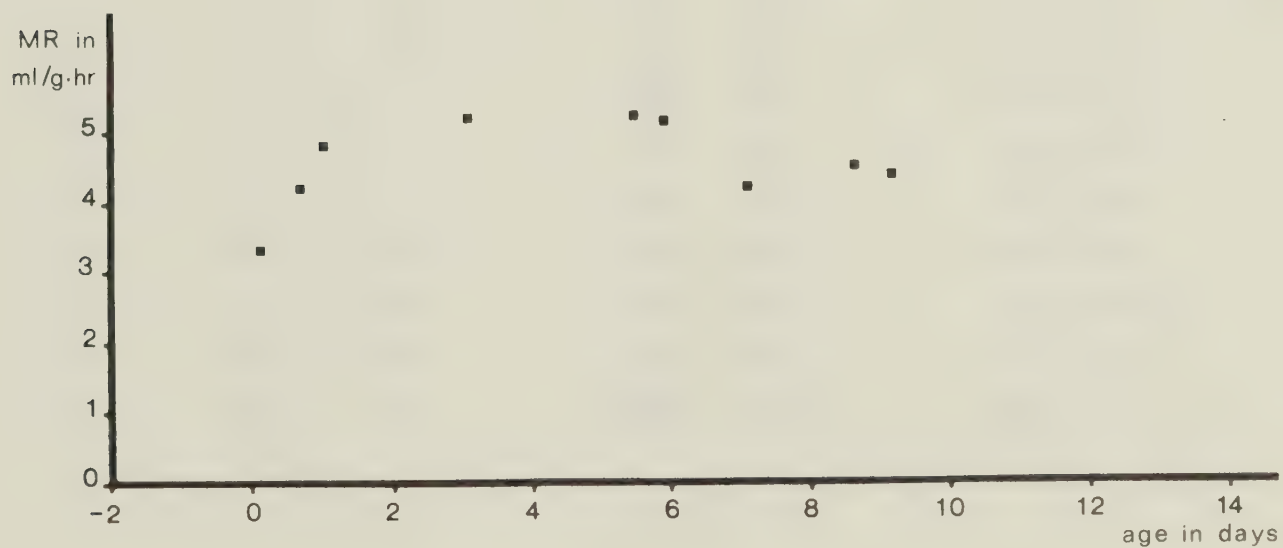
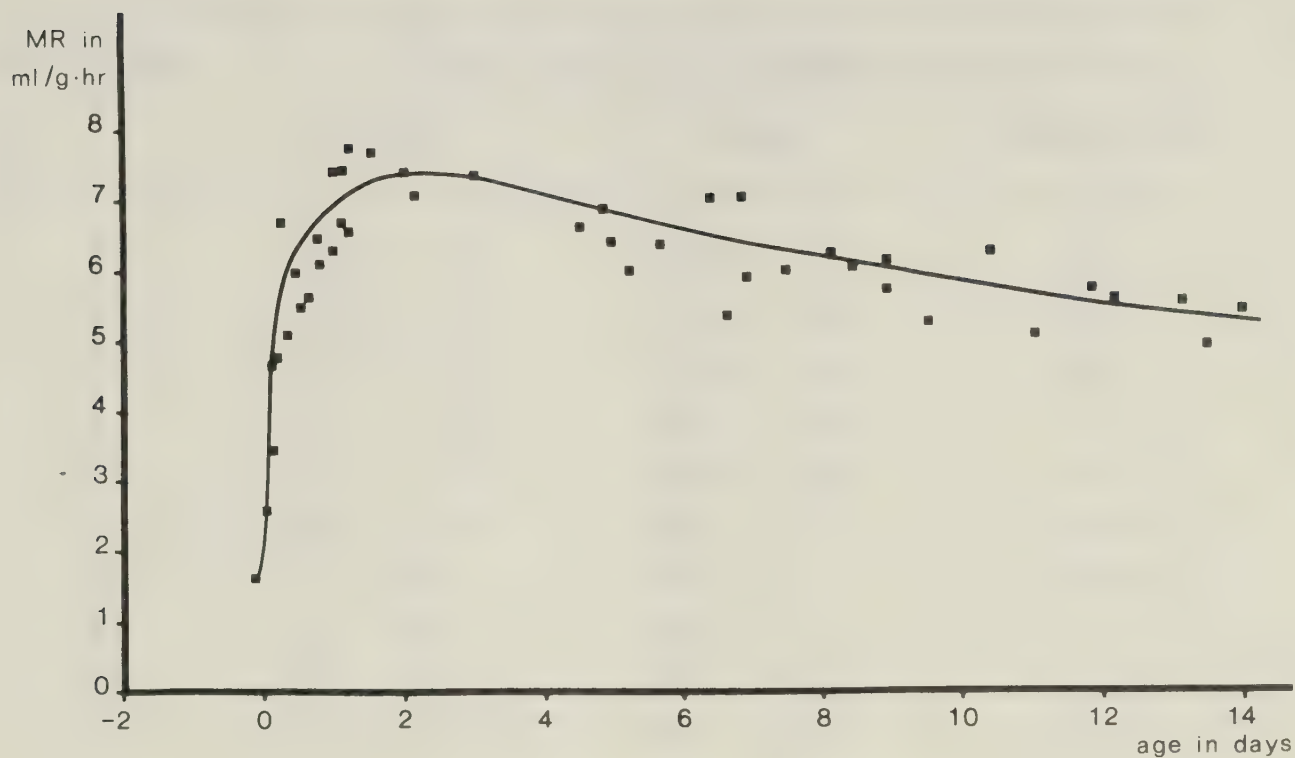


TABLE 2

Weights of ducklings 1 to 20 days old

Age in days	Average weight and standard deviation in g		
	mallard	scaup	common eider
1	30.7 ± 2.9	31.8 ± 1.8	68 ± 8
2	30.7 ± 3.5	32.0 ± 2.5	69 ± 10
3	32.2 ± 4.6	34.9 ± 3.8	70 ± 12
4	35.9 ± 6.4	39.9 ± 5.3	79 ± 12
5	40.7 ± 9.0	46.6 ± 6.4	94 ± 14
6	48.2 ± 11.8	54 ± 8	110 ± 20
7	57 ± 15	61 ± 8	123 ± 24
8	67 ± 18	70 ± 9	141 ± 27
9	79 ± 21	78 ± 10	165 ± 33
10	90 ± 25	87 ± 12	190 ± 36
11	103 ± 28	97 ± 12	211 ± 33
12	120 ± 31	107 ± 13	233 ± 36
13	136 ± 36	119 ± 16	255 ± 38
14	154 ± 41	128 ± 19	280 ± 38
15	174 ± 45	138 ± 21	290 ± 35
16	190 ± 51	149 ± 22	317 ± 41
17	212 ± 56	161 ± 24	335 ± 52
18	230 ± 62	170 ± 24	350 ± 59
19	248 ± 65	182 ± 26	379 ± 64
20	272 ± 71	192 ± 29	420 ± 69

TABLE 3

Scaup: Body composition

age	1 day	1 day	8 days	8 days	15 days	15 days
weight	32.8g	32.9g	60.2g	56.2g	97.1g	142.6g
downy skin	15.7%	15.6%	13.7%	13.8%	15.3%	17.1%
liver + gallbladder	3.8%	5.0%	5.3%	5.7%	5.7%	5.6%
heart	1.2%	1.4%	1.8%	1.8%	1.6%	1.5%
lungs + trachea	2.7%	3.3%	2.7%	2.7%	3.8%	3.3%
digestive tract + spleen	8.9%	10.4%	19.9%	22.0%	19.6%	19.1%
fat	2.1%	1.8%	1.0%	0.9%	1.4%	1.3%
yolk sac	12.5%	9.3%	—	—	—	—
carcass	52.2%	51.7%	53.3%	50.8%	50.2%	50.0%
kidneys	1.3%	1.4%	2.3%	2.2%	2.3%	2.1%

The values calculated are based on the average oxygen consumption observed during the last 30-60 min of an experiment. They are lower than the values observed earlier in the experiment, probably because the organism needs a certain adjustment period during which the metabolism is altered to produce exactly the heat required at the test temperature, and also because the duckling becomes slowly postabsorptive. The values plotted as peak metabolic rates include data obtained at temperatures of up to 3°C above the lowest temperature which a duckling of a given age can normally withstand for 2.5 hours. The graphs shown in Figs. 6 and 7 are drawn close to the highest values obtained because the data undoubtedly include rates which were below the peak values of some ducklings.

The factors involved in the rapid development of thermoregulation during the first day after hatching are unknown. Kendeigh and Baldwin (1928) considered the following points as important factors for the development of thermoregulation in the house wren: the decrease in the proportion of body surface to bulk, development of feathers, development of functional air sacs, increase in total heat production and development of nervous and hormonal control. However, wrens need 2 weeks to become homeothermic while ducklings establish their thermoregulation within a few hours. Therefore changes caused by growth cannot be considered responsible for the establishment of thermoregulation in ducklings. Morphological changes of the nervous system seem unlikely because the time to establish temperature control is so short. The same reasoning applies to hormonal changes. Besides, the age of the embryo at which hatching occurs varies slightly. I found that the noise of the control system in the temperature cabinet stimulated hatching. Pipped scaup eggs hatched earlier in the cabinet than in the brooder, but while the unhatched ducklings showed the

characteristic lack of thermoregulation those which were of the same developmental age but had already hatched started to respond as homeotherms. A duckling tries to sit up as soon as it has hatched and is badly disturbed if one upsets its posture, while the embryo is tolerant to the turning of the egg and the posture change connected with it. It is possible that the freedom of movement triggers some nervous mechanism which influences the thermoregulatory center. Another possibility is that only after hatching do the lungs and air sacs have sufficient space to function at full capacity and supply the blood with the high amount of oxygen required for high metabolic rates. Newly hatched ducklings are able to shiver, but the animals were seldom observed to shiver during an experiment so that it could be felt by hand. Shivering was observed in some chilled ducklings during recovery of their normal body temperature. In the domestic chicken the control of heat production seems to involve the sympathetic nervous system (Wekstein and Zolman, 1969) but the mediator is not norepinephrine (Hart, 1962; Freeman, 1966).

Heat loss decreases considerably shortly after hatching. At hatching the down is wet and lies flat against the body so that it offers no insulation. The down dries within 1 or 2 hours but does not yet provide maximum insulation because at hatching each individual down feather is surrounded by a sheath which has to be rubbed off before the barbs of the feather can unfold and provide the thick down characteristic of ducklings. The time needed for the removal of the sheaths depends on the amount of contact between the ducklings of a clutch—and in nature, also the mother—but is usually 8-12 hours.

An evaluation of the quality of insulation of the species studied is difficult because heat loss is governed by body weight as well as the

quality of the down, and both factors change with age. Overall insulation can be expressed by the equation

$$I_o = \frac{T_b - T_a}{MR} \quad (\text{modified from Scholander } et al., 1950)$$

where I_o = overall insulation index in °C g hr/ml

T_b = body temperature in °C

T_a = ambient temperature in °C

MR = metabolic rate at T_a in ml/g hr.

This equation does not distinguish between the effect of weight on overall insulation and the contribution of the down to insulation. Insulation indices have been calculated and plotted in Figure 9 for all animals from which metabolic rates had been recorded. Between the ages of 1 and 14 days, the relation between age and overall insulation can be expressed by the following equations:

mallards: $Y = 0.53X + 5.03$

scaups: $Y = 0.41X + 5.75$

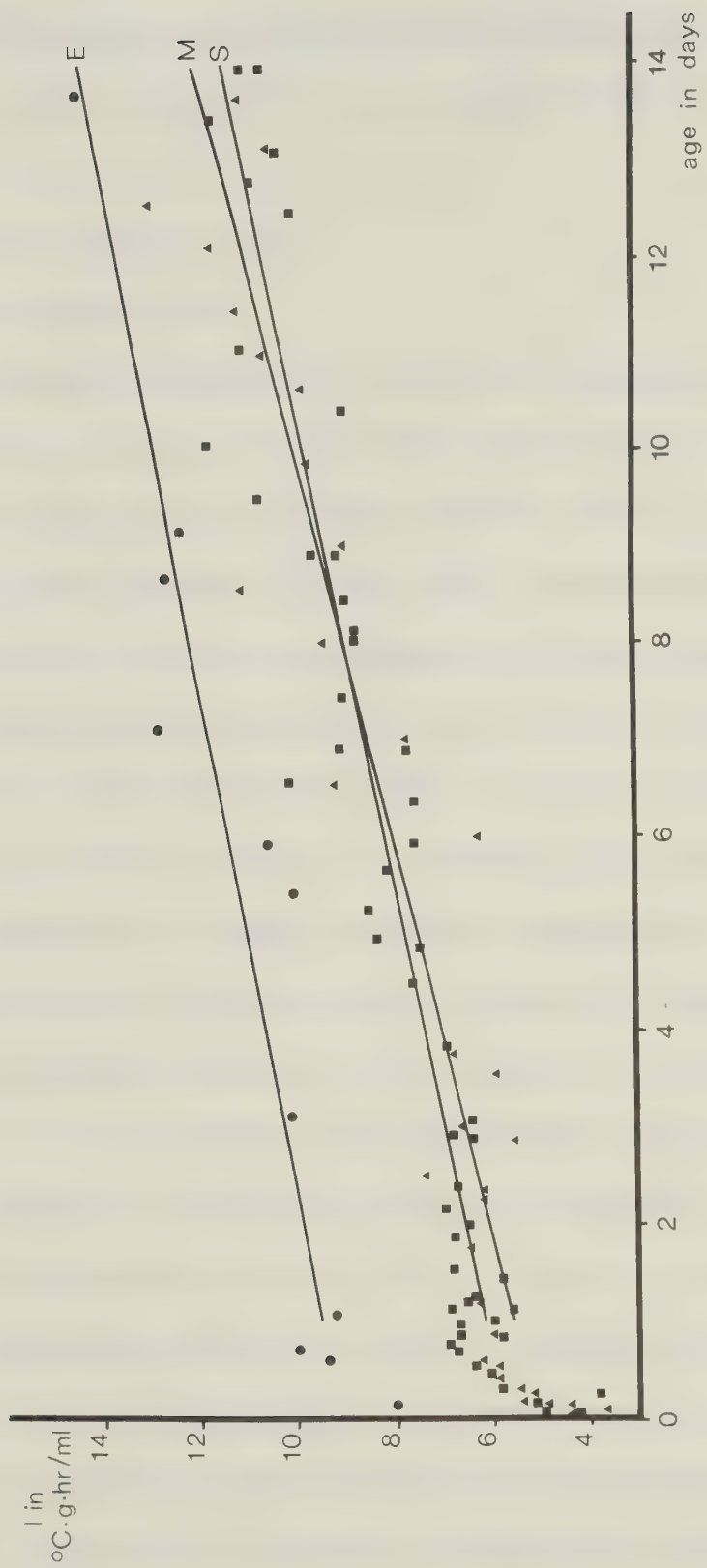
eiders: $Y = 0.44X + 8.52$

where Y = numerical value of the overall insulation index

X = age in days.

The overall insulation indices of mallard and scaup ducklings 1 - 14 days old are significantly different ($\alpha = 0.05$) from those of eider ducklings. There is no significant difference between the overall insulation indices of mallard and scaup ducklings. During the first 2 weeks after hatching, eider ducklings are approximately twice as large as mallard or scaup ducklings of the same age. This raises the question whether the superior overall insulation of eider ducklings is caused by their greater weight or a better quality of the down.

Fig. 9. Changes in overall insulation with age. Triangles: mallards, squares: scaups, dots: eiders. Regression lines were calculated according to the method of least squares. I = overall insulation index in $^{\circ}\text{C g hr/ml}$.



Basal metabolic rates do not increase in a linear way with body weight, and there is no reason to believe that this relation is changed for metabolic rates measured at temperatures below those of the thermoneutral zone. Therefore, insulation indices independent of weight can be calculated if the value of "a" in the equation $BMR = K w^a$ is known, where

BMR = basal metabolic rate,

w = body weight and

K = a constant depending on the units of measurement for BMR and w. Unfortunately, no values for "a" have been reported in the literature for ducks. Koskimies and Lahti (1964) used the value $a = 0.64$ because this factor had been proposed by Brody (1945) who worked on hens, pigeons, sparrows and canaries. Actual measurements of basal metabolic rates in day-old ducklings (Koskimies and Lahti, 1964) gave only 52 - 73% of the values predicted by the formula $BMR = K w^{0.64}$, and the authors concluded that the ducklings were not capable of the heat production characteristic of adults. I disagree with these arguments because the ducklings were obviously homeothermic at thermoneutrality where basal metabolic rates are determined. I conclude instead that the value $a = 0.64$ is not correct for ducklings. I calculated the value of "a" from Koskimies' and Lahti's average basal metabolic rates which had been determined experimentally for 10 species and obtained the value $a = 0.76$. This is close to 0.75 which was found by Kleiber and Dougherty (1934) for domestic chickens 5-14 days old on the basis of food consumption and corresponds to the value generally used to predict mammalian basal metabolic rates (Scholander *et al.*, 1950; Kleiber, 1947). An index of insulation independent of body weight can be calculated according to the formula

$$I = \frac{(T_b - T_a) W^a}{O}, \text{ where}$$

I = weight-independent insulation index in °C g hr/ml

T_b = body temperature in °C

T_a = ambient temperature in °C

O = oxygen consumption per hour

W = weight in g

$a = 0.76$

As metabolic rates in this study have been measured at or close to the lowest temperature which a duckling could withstand while remaining homeothermic the weight-independent insulation indices should represent comparable values for all animals. It is not known whether insulation indices calculated here are maximum values. Veghte and Herreid (1965) found in the gray jay that below the critical temperature insulation first increased but then decreased slightly at temperatures between -27 and -37°C. Corresponding observations on other birds are lacking.

Insulation values independent of body weight have been calculated for all ducklings between 1 and 14 days of age for which metabolic rates had been determined. These values are listed in the appendix. The relation between age and weight-independent insulation index for ducklings 1 - 14 days old can be expressed by the following equations:

mallards: $Y = 0.062X + 2.58$

scaups: $Y = 0.071X + 2.65$

eiders: $Y = 0.022X + 3.54$

where Y = numerical value of the weight-independent insulation index

X = age in days.

The differences among the regression lines are statistically not significant

($\alpha = 0.05$). Therefore, the superior overall insulation of eider ducklings 1 - 14 days old can be attributed mainly to their greater weight.

After the age of 1 day, cold hardiness of all species increases at a fairly constant rate with age for the time during which the animals were studied. The highest peak metabolic rates are reached around the age of 3 days (Figs. 6 and 7) and then decline steadily. The change from the one-day to the 3-day old duckling is associated with the disappearance of the yolk sac and probably does not indicate any change in the metabolic activity of the various tissues but is only an expression of the decrease of inert material in the body. In the domestic chicken, the interatrial perforations close mostly during the first week after hatching (Quiring, 1933). It is possible that this process takes place faster in ducklings than in the chicken and that the change in blood circulation aids in supplying the tissues rapidly with oxygen.

There is no explanation yet for the decrease of the peak metabolic rates after the age of three days. In scaups, changes in the percentage of major body components do not occur over the period the animals were studied (Table 3). The percentage of liver and muscle which are suspected of producing most of the heat (Hart, 1962; Freeman, 1966, 1967) remain nearly constant and do not explain the decrease of the peak value between day 3 and 14. Nothing is known about tissue metabolism in ducklings which might provide the explanation. In domestic chickens which develop cold resistance much more slowly than ducklings, liver homogenates of animals 27-34 days old show metabolic rates more than twice as high as those from younger chickens (5-17 days) or mature females (Crandall and Smith, 1952). In chickens, the highest peak metabolic rates are observed at an older age than in ducklings, but, to judge from data collected by Barott and Pringle

(1946), before the animals are 2 weeks old. The increasing cold hardiness in ducklings over 3 days of age found in this study is caused by a reduction of heat loss resulting mainly from increased weight.

Ducklings are quite tolerant to hypothermia. My experiments were not conducted to study this tolerance, but from a number of ducklings accidentally chilled it appears that mallards up to an age of at least 10 days survive body temperatures of 20°C. Only 2 ducklings died, a 2-day old young which was chilled to a body temperature of 16.5°C and a 4-day old specimen with a body temperature of 12°C. Embryos survive chilling well, but the exact degree of tolerance has not been determined.

Some ducklings had their feet frozen during experiments at very low temperatures. In many cases this had no apparent effect at all. The ducklings seemed to feel no pain, all moved around as easily as before without discomfort. In some animals a discoloration appeared several days after the feet were frozen and some of the horny skin of the feet was shed. In several of these animals tiny pieces of the margin of the web between the toes were lost; this loss amounted only to a few square millimeters and gave the web a somewhat irregular margin.

My research has shown that eider ducklings are the most cold tolerant of the 3 species studied, followed closely by scaups which after the age of 1 day are considerably more cold tolerant than mallard ducklings. Eider ducklings owe their cold resistance to a high body weight and good insulation while scaups exceed mallards by virtue of their higher peak metabolic rates. While the young of all 3 species can withstand severe cold for some hours they do not thrive under such conditions. I observed that even a few cold and rainy days made an impression on the growth curves as intervals during which little or no growth occurred. The cold

tolerance of ducklings helps them to survive short periods of cold weather which can kill the young of many other birds. Jehl and Hussel (1966) observed the effects of a snowstorm of several days on the bird population breeding at Churchill, Manitoba, and found that while most passerine young were destroyed there was no effect on waterfowl reproduction, and broods of normal size and number were seen later in the season.

The difference in cold tolerance between mallards and eiders is without influence on their distribution. Both species are holarctic. The cold tolerance of mallards is obviously sufficient to withstand the adverse conditions in the northern part of their range. Mallard hens keep only their own young in a family group and brood them at regular intervals up to an age of 3 weeks, while scaups and eiders tend to pool their young into community flocks where they receive relatively little individual attention. The differences in physiological traits are therefore at least partially balanced by differences in behaviour.

REFERENCES

- Barott, H.G. and E.M. Pringle 1946. Energy and gaseous metabolism of the chicken from hatch to maturity as affected by temperature. *J. Nutrition* 31: 35-50.
- Barry, T.W. 1967. Geese of the Anderson River Delta, Northwest Territories. Thesis at U. of A.
- Brody, S. 1945. Bioenergetics and growth. Reinhold Publish. Corp.: New York.
- Crandall, R.R. and A.H. Smith 1952. Tissue metabolism in growing birds. *Proc. Soc. for Exp. Biol. and Med.* 79: 345-346.
- Freeman, B.M. 1966. The effects of cold, noradrenaline and adrenaline upon the oxygen consumption and carbohydrate metabolism of the young fowl (*Gallus domesticus*). *Comp. Biochem. Physiol.* 18: 369-382.
- Freeman, B.M. 1967. Some effects of cold on the metabolism of the fowl during the perinatal period. *Comp. Biochem. Physiol.* 20: 179-193.
- Hart, J.S. 1962. Seasonal acclimatization in 4 species of small wild birds. *Physiol. Zool.* 35: 224-236.
- Huggins, R. 1941. Egg temperatures of wild birds under natural conditions. *Ecology* 22: 148-157.
- Irving, L. and J. Krog 1955. Temperature of skin in arctic as a regulator of heat. *J. applied Physiol.* 7: 355-364.
- Jehl, J.R. and D.J.T. Hussen 1966. Effects of weather on reproductive success of birds at Churchill, Manitoba. *Arctic* 19: 185-191.
- Kendeigh, S.C. 1939. The relation of metabolism to the development of temperature regulation in birds. *J. exp. Zool.* 82: 419-438.
- Kleiber, M. 1947. Body size and metabolic rate. *Physiol. Reviews* 27: 511-541.

- Kleiber, M. and J.E. Dougherty 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. *J. gen. Physiol.* 17: 701-726.
- Koch, A. and L. Steinke 1944. Temperatur-und Feuchtigkeitsmessungen im Brutnest von Gänsen, Puten und Hühnern. *Beiträge zur Fortpflanzungsbiologie der Vögel* 20: 41-45.
- Koskimies, J. 1962. Ontogeny of thermoregulation and energy metabolism in some gallinaceous birds. *Trans. 5th Congress Intern. Union Game Biol., Bologna*, pp. 149-160.
- Koskimies, J. and L. Lahti 1964. Cold hardiness of the newly hatched young in relation to the ecology and distribution in ten species of European ducks. *Auk* 81: 281-307.
- Pembry, M.S., M.H. Gordon and R. Warren 1895. On the response of the chick, before and after hatching, to change of external temperature. *J. Physiol. (London)* 17: 331-348.
- Quiring, D.P. 1933. The development of the sino-atrial region of the chick heart. *J. Morph.* 55: 81-118.
- Rolnik, V.V. 1948. Development of thermoregulation in some birds of the North. *Zool. J.* 27: 535-546. In Russian.
- Scholander, P.F., R. Hock, V. Walters, F. Johnson and L. Irving 1950. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* 99: 237-258.
- Scholander, P.F., R. Hock, V. Walters and L. Irving 1950. Adaptations to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.* 99: 259-271.
- Sokal, R.R. and F.J. Rohlf 1969. *Biometry*. W.H. Freeman and Co.: San Francisco.

- Veghte, J.H. and C.F. Herreid 1965. Radiometric determination of feather insulation and metabolism of arctic birds. *Physiol. Zool.* 38: 267-275.
- Wekstein, D.R. and J.F. Zolman 1967. Homeothermic development of the young chick. *Proc. of the Soc. for exp. Biol. and Med.* 125: 294-297.
- Wekstein, D.R. and J.F. Zolman 1969. Ontogeny of heat production in chicks. *Federation Proceed.* 28: 1023-1028.

APPENDIX

Metabolic rates of embryos

Mallards

Time before hatching (days - hours)	Weight of embryo in g	Ambient temp. in °C	Metabolic rate in ml/g hr
0 - 2.5	35.4	33.7	1.23
0 - 1.5	"	36.1	1.33
0 - 1.5	"	37.6	1.31
0 - 7	35.4	37.6	1.31
0 - 6	"	39.2	1.29
0 - 5	"	41.0	1.34
ca 0 - 12	34.7	27.5	0.49
"	"	29.5	0.53
"	"	32.5	0.72
"	"	34.7	0.79
"	"	36.3	0.96
"	"	37.7	1.01
"	"	39.8	0.90
ca 1 - 0	31.2	28.0	0.43
"	"	30.5	0.56
"	"	32.9	0.72
"	"	35.4	0.86
"	"	36.9	0.96
"	"	38.5	1.05
"	"	40.2	1.08
1 - 8	36.6	34.0	0.99
1 - 7	"	37.2	1.09
1 - 6	"	38.7	1.12
1 - 5	"	40.3	1.18
1 - 5	"	40.7	1.12
1 - 4	"	41.6	1.03
2 - 0	25.4	28.4	0.60
"	"	31.0	0.76
"	"	33.5	0.84

APPENDIX (Cont'd)

Time before hatching in days	Weight of embryo in g	Ambient temp. in °C	Metabolic rate in ml/g hr
2	25.4	35.8	0.94
"	"	38.4	0.94
"	"	40.0	0.95
"	"	42.2	0.91
3	25.6	27.8	0.44
"	"	30.4	0.58
"	"	32.0	0.65
"	"	34.5	0.71
"	"	37.3	0.91
"	"	39.5	1.01
"	"	41.6	0.97
"	"	43.0	0.99
3	22.9	32.4	0.76
"	"	34.6	0.85
"	"	36.8	0.91
"	"	39.3	1.00
4	19.9	18.4	0.15
"	"	26.2	0.38
"	"	30.3	0.70
"	"	38.0	1.09
4	18.3	34.7	1.06
"	"	37.0	1.20
"	"	39.0	1.26
"	"	40.4	1.29
"	"	41.9	1.28
4	19.1	30.5	0.84
"	"	33.3	1.03
"	"	36.3	1.10
"	"	39.0	1.21
"	"	40.8	1.23
"	"	42.1	1.19
"	"	43.1	1.22

....

APPENDIX (Cont'd)

Time before hatching in days	Weight of embryo in g	Ambient temp. in °C	Metabolic rate in ml/g hr
5	19.6	28.3	0.62
"	"	30.2	0.79
"	"	32.8	1.09
"	"	35.4	1.18
"	"	36.9	1.24
"	"	38.4	1.25
"	"	40.1	1.32
7	11.0	27.8	0.68
"	"	36.0	1.19

(days - hours)

Scaups

0 - 4	33.2	33.3	1.16
0 - 2	"	35.3	1.31
0 - 6	34.7	33.0	0.95
0 - 5	"	35.0	1.03
0 - 3	"	36.0	1.15
0 - 1	"	37.7	1.40
0 - 7	34.1	35.1	1.25
0 - 4	"	36.4	1.33
0 - 3	"	37.9	1.50
0 - 2	"	39.0	1.63
0 - 3	37.2	35.3	1.20
0 - 1	"	37.2	1.24

Eiders

ca	0 - 12	70.3	36.4	0.98
	0 - 12	84.5	29.6	0.93
	"	"	36.4	1.02

APPENDIX (Cont'd)

Metabolic rates of ducklings

Mallards

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of cold test	Metabolic rate in ml/g hr	Insulation index
0		31.0	-		
0 - 0.5	36.7	31.6	+	2.21	1.61
0 - 0.5	32.6	33.8	+		
0 - 1	36.2	30.5	+	2.22	1.81
0 - 2	33.6	31.3	+	2.43	1.55
0 - 2		27.0	+		
0 - 2		29.4	+		
0 - 3	33.9	28.5	+	2.67	1.85
0 - 3	28.7	25.3	+	3.10	2.12
0 - 4	33.0	21.6	+	3.47	2.30
0 - 4	29.1	24.4	-		
0 - 5		22.6	-		
0 - 6	30.6	25.0	+	2.95	2.24
0 - 7	31.9	16.8	+	4.33	2.34
0 - 10	34.3	13.1	+	4.65	2.48
0 - 11	29.5	3.5	-		
0 - 12		22.6	+		
0 - 13	34.6	5.6	+	5.94	2.48
0 - 13		4.3	-		
0 - 14	33.2	-1.0	-		
0 - 15	31.5	7.5	+	5.31	2.68
0 - 15	26.4	9.4	+		
0 - 15	28.2	9.4	+		
0 - 15	27.5	9.4	+		
0 - 16		4.3	-		
0 - 17		4.3	+		
0 - 20	28.4	-0.8	-		
0 - 21	30.2	3.8	+	6.13	2.60
0 - 22	32.0	-1.0	-		
0 - 22	27.6	2.6	-		
0 - 23	32.1	4.1	-		
1 - 4	29.0	0.7	+	6.36	2.66

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of Metabolic rate cold test in ml/g hr	Insulation index
1 - 9	32.2	2.2	+	
1 - 9	28.6	2.2	+	
1 - 12	26.2	4.0	+	
1 - 12	37.0	-2.0	-	
1 - 17	36.3	-2.0	-	
1 - 18	30.3	-2.0	-	
1 - 18	30.2	-0.5	+	6.37 2.80
2 - 1	32.8	-1.0	-	
2 - 1	28.2	-3.3	-	
2 - 6	28.4	2.2	+	
2 - 6	28.8	-0.4	+	6.65 2.73
2 - 7	30.5	-0.5	+	6.64 2.68
2 - 11	34.0	0	+	
2 - 12	33.0	0	-	
2 - 12	37.4	-1.2	+	5.64 3.07
2 - 18	27.1	2.2	-	
2 - 19	39.0	0	-	
2 - 20	32.5	2.3	+	6.64 2.46
3 - 0	40.5	-3.3	+	6.56 2.82
3 - 11	33.0	-2.0	-	
3 - 13	33.3	-0.8	+	7.00 2.52
3 - 15	38.0	-2.0	-	
3 - 17	32.1	1.8	-	
3 - 18	34.7	-2.8	+	6.32 2.89
3 - 19	28.0	-3.5	-	
4 - 1	32.2	-2.6	-	
4 - 8	47.0	-1.5	-	
4 - 12	53.1	-5.8	-	
4 - 14	41.0	-1.5	+	
4 - 15	52.0	-1.5	-	
5 - 0	42.1	-1.5	-	
5 - 17	48.4	-2.1	-	

....

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of Metabolic rate cold test	Insulation index
5 - 23	51.8	-4.6	-	
6 - 0	41.2	-2.3	+	6.78 2.56
6 - 13	73.4	-3.7	+	4.79 3.26
7 - 0	67.2	-3.1	+	5.59 2.82
7 - 13	73.8	-5.4	-	
7 - 13	44.0	-4.6	-	
7 - 13	72.0	-4.6	+	
7 - 15	52.7	-2.8	-	
7 - 21	74.0	-4.6	+	
8 - 0	60.9	-5.8	-	
8 - 0	96.2	-5.3	+	4.81 3.16
8 - 12	99.0	-7.5	+	
8 - 13	124	-7.2	+	4.26 3.48
8 - 15	70.0	-7.5	-	
8 - 18	75.0	-7.5	-	
9 - 0	81.5	-6.2	+	5.15 3.12
9 - 11	74.0	-7.0	-	
9 - 18	63.0	-7.0	-	
9 - 21	117	-9.0	+	5.05 3.09
10 - 12	121	-7.0	+	
10 - 13	62.0	-7.0	-	
10 - 15	109	-9.2	+	5.00 3.18
10 - 16	131	-9.4	-	
10 - 20	119	-7.0	-	
10 - 23	64.0	-8.0	-	
11 - 0	120	-11.0	-	
11 - 0	109	-9.1	+	4.61 3.45
11 - 11	153	-9.5	+	4.43 3.34
12 - 3	141	-10.5	+	4.33 3.55
12 - 7	108	-8.0	-	
12 - 13	212	-12.5	+	4.06 3.56

....

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of cold test	Metabolic rate in ml/g hr	Insulation index
12 - 17	118	-8.0	-		
13 - 3	156	-10.6	+	4.82	3.12
13 - 16	182	-13.3	+	4.82	3.17
14 - 2	132	-7.8	+	4.78	3.10
14 - 5	131	-8.5	+	4.70	3.21
14 - 6	214	-13.3	+	4.33	3.39
14 - 7	229	-15.0	+	4.38	3.40
14 - 12	140	-10.4	-		
15 - 0	247	-15.0	+	2.94	
15 - 1	190	-15.0	+	2.99	
15 - 6	147	-12.4	+		
15 - 11	139	-13.0	-		
15 - 11	220	-12.8	+		
15 - 16	216	-10.4	+		
15 - 16	261	-10.4	+		
15 - 18	118	-13.5	-		
15 - 22	201	-15.0	+	3.50	
16 - 8	212	-12.3	+	4.22	
16 - 19	237	-14.5	+		
17 - 1	271	-16.6	+	2.45	
17 - 8	118	-16.9	-		
17 - 8	297	-16.9	+		
17 - 11	253	-17.0	+	2.49	
17 - 15	322	-14.5	+		
17 - 16	267	-18.0	+	3.46	
18 - 2	264	-17.3	+	3.29	
18 - 12	317	-16.9	+		
Scaups					
0 - 1	39.0	19.8	-		
0 - 1	38.1	29.1	+	2.60	1.75
0 - 2	37.5	27.6	+		

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of Metabolic rate cold test in ml/g hr	Insulation index
0 - 2	36.0	14.5	-	
0 - 2	36.5	11.4	-	
0 - 2	34.0	17.2	+	4.64 2.11
0 - 3	32.4	23.2	+	3.46 2.11
0 - 4	32.7	16.0	+	4.78 2.18
0 - 6	32.0	23.2	+	
0 - 6	32.9	14.7	+	6.69 1.63
0 - 8	30.2	9.0	-	
0 - 8	34.7	10.5	+	5.11 2.46
0 - 11	32.3	4.6	+	5.95 2.58
0 - 13	32.6	5.1	+	5.52 2.74
0 - 13	30.7	4.0	-	
0 - 15	33.4	2.4	+	5.62 2.89
0 - 17	30.6	8.5	+	5.38 2.58
0 - 18	34.6	-4.4	+	6.45 2.94
0 - 20	33.6	0.4	+	6.11 2.86
0 - 21	29.8	-8.6	-	
0 - 23	33.2	1.7	+	6.28 2.84
1 - 0	29.2	-4.0	+	7.40 2.65
1 - 3	32.9	-1.2	+	7.43 2.41
1 - 3	31.8	-5.7	+	6.66 3.00
1 - 6	30.9	-1.5	+	6.53 2.80
1 - 6	33.6	-10.0	+	7.71 2.80
1 - 11	29.1	0.2	+	6.93 2.57
1 - 13	32.6	-11.9	+	7.68 2.92
1 - 17	31.4	-14.5	-	
1 - 19	33.7	-6.5	-	
1 - 20	28.2	0.6	-	
1 - 21	34.1	-2.9	+	6.35 2.89
2 - 0	37.2	-7.8	+	7.39 2.71
2 - 4	36.7	-9.4	+	7.06 2.96

....

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of Metabolic rate cold test in ml/g hr	Insulation index
2 - 10	37.5	-3.7	+	2.81
2 - 12	34.9	-6.4	-	
2 - 14	30.7	-10.2	-	
2 - 22	37.9	1.2	+	2.66
2 - 23	34.3	-9.5	+	2.89
3 - 2	39.1	-4.7	+	2.65
3 - 10	43.1	-12.0	-	
3 - 17	36.5	-10.0	-	
3 - 20	43.6	-4.8	+	2.80
4 - 3	45.8	-10.0	-	
4 - 5	47.3	-13.5	-	
4 - 11	43.2	-8.0	-	
4 - 11	43.0	-6.6	-	
4 - 12	54.0	-10.2	+	2.91
4 - 20	54.9	-11.3	+	2.85
4 - 23	49.5	-13.2	+	3.26
5 - 6	61.0	-11.0	+	3.16
5 - 16	55.7	-12.0	+	3.11
5 - 17	50.5	-14.3	-	
5 - 23	50.3	-8.0	+	2.95
6 - 4	55.6	-14.4	-	
6 - 9	49.8	-13.0	+	2.95
6 - 15	61.1	-14.0	+	3.79
6 - 21	54.4	-14.0	+	2.94
6 - 22	60.9	-13.2	+	3.36
6 - 23	54.7	-15.3	-	
7 - 11	72.6	-14.0	+	3.23
8 - 1	70.2	-8.5	+	3.15
8 - 2	65.3	-14.7	+	3.22
8 - 3	70.8	-16.0	-	
8 - 10	76.2	-14.0	-	
8 - 11	86.0	-14.1	+	3.07

....

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of Metabolic rate cold test	Metabolic rate in ml/g hr	Insulation index
8 - 22	85.0	-15.2	+	5.72	3.33
8 - 22	86.6	-16.2	+	6.14	3.14
9 - 12	104	-15.6	+	5.26	3.53
10 - 1	97.9	-11.3	+	4.35	3.93
10 - 10	74.2	-16.1	+	6.24	3.20
10 - 12	86.0	-17.5	-		
11 - 1	118	-16.8	+	5.10	3.55
11 - 11	82.6	-17.5	-		
12 - 12	102	-17.5	+	5.72	3.31
12 - 19	127	-20.7	+	5.57	3.41
13 - 2	129	-17.6	+	5.55	3.23
13 - 4	122	-20.3	-		
13 - 11	131	-17.5	+	4.92	3.63
13 - 23	119	-20.0	+	5.45	3.50
14 - 2	136	-20.7	+		

Eiders

0	79.2	18.3	-		
0	74.8	24.5	-		
0 - 2	68.7	14.5	-		
0 - 2	85.0	25.5	+		
0 - 3	71.7	25.5	+		
0 - 3	71.6	13.7	+	3.32	2.84
0 - 10	75.8	0.7	-		
0 - 14	74.7	5.3	+	3.74	3.29
0 - 16	68.2	-1.0	-		
0 - 17	67.6	-2.0	+	4.23	3.61
0 - 18	72.8	-4.1	-		
0 - 20	64.2	-5.8	+		
1 - 1	57.2	-7.0	+	5.15	3.46
1 - 4	73.2	0.7	+		

....

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of cold test	Metabolic rate in ml/g hr	Insulation index
1 - 4	66.5	0.7	+		
1 - 4	72.6	-16.3	-		
1 - 7	77.6	-8.3	+		
1 - 8	69.9	-10.2	-		
1 - 9	54.2	-5.8	+		
1 - 20	88.3	0.7	+		
1 - 21	76.1	-5.8	+		
2 - 0	59.1	-13.0	-		
2 - 1	74.6	-10.2	+		
3 - 2	69.2	-12.2	+	5.20	3.63
3 - 6	57.4	-11.0	+		
3 - 6	66.8	-11.0	+		
3 - 8	75.6	-16.0	-		
3 - 10	64.8	-14.9	-		
3 - 13	64.4	-10.2	+		
3 - 18	82.9	-11.0	+		
3 - 23	85.0	-16.0	-		
4 - 2	74.2	-13.0	+		
4 - 3	101	-14.2	+		
4 - 22	68.9	-14.0	-		
5 - 10	74.6	-12.2	+	5.23	3.54
5 - 20	127	-16.3	-		
5 - 21	67.7	-15.0	-		
5 - 22	87.8	-14.0	-		
5 - 22	98.8	-14.4	+	5.15	3.54
6 - 6	156	-13.0	+		
7 - 2	115	-14.0	+	4.22	4.09
7 - 6	103	-14.9	+		
7 - 15	123	-14.2	+		
8 - 15	142	-16.8	+	4.49	3.85
8 - 16	173	-14.2	+		
8 - 20	182	-16.0	+		

APPENDIX (Cont'd)

Age (days - hours)	Body weight in g	Ambient temp. in °C	Result of cold test	Metabolic rate in ml/g hr	Insulation index
9 - 4	143	-14.2	+	4.38	3.76
9 - 14	195	-16.0	+		
9 - 18	175	-13.0	+		
10 - 1	210	-14.9	+		
10 - 14	176	-17.6	+		
11 - 3	206	-18.0	+		
11 - 7	265	-20.2	+		
13 - 16	300	-18.2	+		
13 - 16	301	-15.0	+	3.81	3.67
14 - 6	240	-18.0	+		
15 - 4	313	-20.0	+		
15 - 8	303	-20.2	+		
16 - 5	400	-20.0	-		
16 - 6	344	-22.0	+		
16 - 22	376	-22.0	+		

B30001